

# Epomophorus gambianus. By Margaret C. Boulay and C. Brian Robbins

Published 26 October 1989 by The American Society of Mammalogists

## Epomophorus Bennett, 1836

*Pteropus* Ogilby, 1835:100 (not *Pteropus* Erxleben, 1777).

*Epomophorus* Bennett, 1836a:149. Type species *Pteropus epomophorus* Bennett, by monotypy (= *Pteropus gambianus* Ogilby).

*Pachysoma* Temminck, 1853:64 (not *Pachysoma* I. Geoffroy Saint-Hilaire, 1828; name preoccupied by *Pachysoma* MacLeay, 1821, a genus of Coleoptera).

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Subfamily Pteropodinae, Genus *Epomophorus*. The genus *Epomophorus* contains six species (Bergmans, 1988). The following key is adapted from measurements (in mm) of Hayman and Hill (1971), Koopman (1975), and Bergmans (1988).

- 1 Single strong transverse palatal ridge between last molars and upturned posterior edge of bony palate (bony support usually evident even if ridge cleaned of tissue); one postdental palatal ridge, length of forearm 72 to 95 (males), 68 to 88 (females) ..... *E. wahlbergi*
- Two weaker transverse parallel palatal ridges between last molars and upturned posterior edge of bony palate (bony supports faint if bony palate cleaned); two postdental fleshy palatal ridges ..... 2
- 2 Second to fourth fleshy palatal ridge divided in the middle; length of forearm 62.3 to 62.8 (males), 65.8 (females) ..... *E. grandis*
- Second to fourth fleshy palatal ridges undivided ..... 3
- 3 Fourth fleshy palatal ridge nearer third than fifth; western Angola, north-western Namibia ..... *E. angolensis*
- Fourth fleshy palatal ridge midway between third and fifth ..... 4
- 4 Condylobasal length 51.1 to 63.6 (males), 45.0 to 56.1 (females) ..... *E. gambianus*
- Condylobasal length less than 50 (males), 45 (females) ..... 5
- 5 Condylobasal length 40.0 to 48.4 (males), 37.0 to 43.9 (females) ..... *E. labiatus*
- Condylobasal length usually less than 40 (33.0 to 40.8 in males and 31.0 to 39.0 in females) ..... *E. minor*

## Epomophorus gambianus (Ogilby, 1835)

### Gambian Epauleted Bat

*Pteropus gambianus* Ogilby, 1835:100. Type locality "Gambia."

*Pteropus macrocephalus* Ogilby, 1835:101. Type locality "Gambia."

*Pteropus megacephalus* Swainson, 1835:92. Type locality "Western Africa."

*Pteropus epomophorus* Bennett, 1836a:149. Type locality "in regione Gambiensi."

*Pteropus whitei* Bennett, 1836b:37. Type locality "in regione Gambiensi."

*Epomophorus whitii*: Gray, 1838:504. Name combination and incorrect subsequent spelling of *Pteropus whitei* Bennett.

*Epomophorus gambianus*: Gray, 1838:504. First use of current name combination.

*Epomophorus crypturus* Peters, 1852:26. Type locality "Tete" (Mozambique).

*Pachysoma whitei*: Temminck, 1853:65. Name combination.

*Pachysoma gambianus*: Temminck, 1853:69. Name combination.

*Pachysoma macrocephala*: Temminck, 1853:70. Name combination.

*Pt[eropus (Pachysoma)] crypturus*: Wagner, 1855:605. Name combination.

*Pt[eropus (Pachysoma)] macrocephalus*: Wagner, 1855:606. Name combination.

*Pt[eropus (Pachysoma)] gambianus*: Wagner, 1855:607. Name combination.

*Pt[eropus (Pachysoma)] whitei*: Wagner, 1855:607. Name combination.

*Epomophorus guineensis* Bocage, 1899:136. Type locality "Boulama (Barahona)," Portuguese Guinea.

*Epomophorus zechi* Matschie, 1899:46. Type locality "Accra, Goldkuste [= Ghana], Gross-Popo, Misahöhe in Togoland, Lagos [Nigeria]," restricted to Kunjuruma, Togoland [= Benin] by Andersen (1912).

*Epomophorus pousarguesi* Trouessart, 1904:55. Type locality "Africa Occ.-Centrali, ad fl. Chari (inter Yabanda et Mpoko), Reg. Lac. Tchad," Central African Republic; restricted to 'along the track between Mpoko (near Makorou) and Yabanda' by Bergmans (1978b).

*Epomophorus reii* Aellen, 1950:559. Type locality "Rei Bouba", Cameroon.

**CONTEXT AND CONTENT.** Context as in the generic summary. There are three currently recognized subspecies (Bergmans, 1988):

*E. g. gambianus* (Ogilby, 1835:100), see above (*macrocephalus* Ogilby, *megacephalus* Swainson, *whitei* Bennett, *whitii* Gray, *guineensis* Bocage, *zechi* Matschie, and *reii* Aellen are synonyms).

*E. g. crypturus* Peters, 1852:26, see above (*parvus* Ansell is a synonym).

*E. g. pousarguesi* Trouessart, 1904:55, see above.

**DIAGNOSIS.** The fleshy palatal ridges evident on uncleaned skulls are used to distinguish *Epomophorus* from other pteropodids and to differentiate the species of *Epomophorus*. *E. gambianus* resembles *Epomops frangueti*, but may be differentiated by its more elongate head and six palatal ridges. *E. gambianus* has four interdental and two postdental palatal ridges. *E. frangueti* has a rounded head and three prominent interdental and five or six less prominent postdental ridges. The posterior palates of species of *Epomophorus* are deeply hollowed; those of species of *Epomops* are shallow or flattened.

The distribution of *E. gambianus* overlaps those of *E. wahlbergi*, *E. grandis*, *E. minor*, and *E. labiatus*. *E. gambianus* can be distinguished from these species using characters of the palate, length of forearm, or condylobasal length. The bony palate of *E. gambianus* has two weakly-developed transverse-parallel ridges between M1 and the upturned posterior edge of the palate, whereas the bony palate of *E. wahlbergi* has one well-developed transverse ridge. *E. wahlbergi* is the only species of *Epomophorus* having five fleshy interdental ridges and one postdental ridge, in contrast to the four interdental and two postdental ridges of the other species.

The second to fourth palatal ridges of *E. gambianus* are not interrupted in the middle. Those of *E. grandis* are divided. *E. gambianus* may be further differentiated from *E. grandis* by its larger size. *E. gambianus* has a length of forearm of 80 to 100 for males, 75.0 to 94.8 for females, whereas *E. grandis* has a length of forearm of 62.3 to 62.8 for males, 65.8 for females.

*Epomophorus gambianus* is larger than both *E. labiatus* and *E. minor*, having a condylobasal length (in mm) >50 for males and >45 for females, whereas those of both *E. minor* and *E. labiatus* are <50 for males and <45 for females.

The range of *E. gambianus* does not overlap that of *E. angolensis*. *E. angolensis* occurs in western Angola and northwestern Namibia. The position of the palatal ridges can be used to differentiate *E. gambianus* from *E. angolensis*. The fourth palatal ridge of *E. gambianus* lies midway between the third and fifth ridges, whereas



FIG. 1. *Epomophorus gambianus*, photographed in Ghana, West Africa by B. J. Hayward.

the third and fourth palatal ridges of *E. angolensis* are nearer to each other than to either the second or fifth ridges.

**GENERAL CHARACTERS.** *Epomophorus gambianus* is medium sized for species within its family. The head is large and elongate with a gradually tapering muzzle. The lips are well developed and fleshy; the upper lip is extensible (Fig. 1). The nose forks into a "Y" at the tip, and the nostrils are enlarged and padded. The ears are medium to dark brown, and are fairly large with slightly convex margins and broadly rounded tips. The interfemoral membrane is narrow, forming an inverted "V" shape. The tail usually is not detectable, although some individuals may have tails as long as 6 mm (Rosevear, 1965).

*Epomophorus gambianus* shows secondary sexual dimorphism. Males are larger and have epaulets, which are thick tufts of long white hairs growing within circular pocket-like folds of skin on the shoulders. Normally folded into the pouch-like folds of skin, the hairs form a conspicuous white rosette when everted. Subadult males do not have fully-developed epaulets (Rosevear, 1965).

The dorsal color is brownish fawn-color, varying from prout's brown to fawn-wood brown, with most individuals an intermediate shade, named cafe-au-lait by Andersen (1912; color nomenclature follows Ridgway, 1912). The head, neck, and back may have a reddish-brown tint. These variations are not due to vegetation and climate alone; a specimen from a dryer area was reported to be darker than those from a more mesic area (Rosevear, 1965), and darkest and palest extremes have been represented in specimens collected from one locality during the same season (Andersen, 1912). The ventral color is often paler and more variable than the dorsal ranging from shades similar to the dorsal pelage to all white. Adults may have an abdominal patch of grayish hairs at the center of the ventrum. Rosevear (1965) reported one specimen from Gambia having a yellow venter and orange hairs around the neck. The pelage extends to the upper arms and half of the forearms, both dorsally and ventrally, and to the full extent of the legs dorsally and half ventrally. Hairs on the wing membranes and interfemoral membrane are the dorsal color and dense above, paler and more sparse below. White basal ear tufts occur both anterior and posterior to the ear, with the anterior tufts larger and more visible (Rosevear, 1965).

Ranges for external measurements (in g or mm) for males and females, respectively, are: mass, 91 to 155, 56 to 145; total length, 155 to 197, 131 to 173; length of forearm, 80 to 100, 75 to 95; length of thumb, 36 to 40, 34 to 39; length of metacarpal of digit II, 42 to 46, 40 to 45; length of phalanx I, 8 to 11, 8 to 10; length of phalanges II and III, 11 to 13, 10 to 13; length of metacarpal of digit III, 61 to 67, 56 to 63; length of phalanx, 39 to 42, 37 to 41; length of phalanx II, 52 to 60, 49 to 55; length of metacarpal of digit IV, 58 to 62, 53 to 60; length of phalanx I, 28 to 31, 27 to 30; length of phalanx II, 31 to 35, 30 to 33; length of metacarpal of digit V, 57 to 62, 53 to 61; length of phalanx I, 26 to 30, 27 to 30; length of phalanx II, 28 to 32, 26 to 31; length of ear from notch, 22 to 25, 22 to 24; greatest width of ear, flattened, 16 to 19, 15 to 17; length of tail, 0 to 6, 0 to 6; depth of interfemoral membrane in center, 4 to 9, 3 to 8; length of tibia, 33 to 41, 32 to 37; length of foot, 23 to 26, 22 to 26; length of calcus, 8 to 11, 7 to 11 (Andersen, 1912; Bergmans, 1988; DeVree, 1971; Rosevear, 1965).

The skull (Fig. 2) is long and narrow, especially in males, due to the long rostrum. The length of the rostrum, from the front of the orbit to tip of nasals, is much greater than the width across crowns of M1. The front of the orbit in both sexes is considerably behind M1. The braincase is flat, slopes downward posteriorly, and has a weak sagittal crest. Lambdoidal crests and supraorbital processes are well developed. Ranges of skull measurements (in mm) for males and females, respectively, are: total length of skull, 51 to 64, 44 to 57; condylobasal length, 51 to 64, 44 to 57; length of palatine to incisive foramina, 32 to 38, 29 to 32; length of postdental palate, 15 to 17, 12 to 15; front of orbit to tip of nasals, 24 to 27, 21 to 23; width of braincase at zygomata, 18 to 20, 17 to 18; zygomatic width, 25 to 32, 23 to 29; length of rostrum, 22 to 30, 18 to 26; length between first canine and first molar, 16 to 24, 14 to 24; width across crowns of M1, externally, 14 to 16, 13 to 15; width across crowns of canines, externally, 10 to 12, 9 to 11; length of mandible from condyle, 47 to 51, 40 to 45; length of maxillary toothrow, 20 to 24, 18 to 20 (Allen, 1952; Andersen, 1912; Bergmans, 1988; DeVree, 1971; Rosevear, 1965).

The dental formula is  $i\ 2/2$ ,  $c\ 1/1$ ,  $p\ 2/3$ ,  $m\ 1/2$ , total 28. The upper canine and first upper premolar are recurved and pointed. The lower cheekteeth are not lobed, and the second lower premolars are subcaniniform. The fifth palatal ridge (anterior post-dental) is just behind the tooth row; the sixth is anterior to the middle of the postdental palate (Rosevear, 1965).

**DISTRIBUTION.** *Epomophorus gambianus gambianus* is common throughout savannas and woodlands of western Africa, occurring from Senegal to southern Sudan and southern Ethiopia (Bergmans, 1978b; Hayman and Hill, 1971; Rosevear, 1965; Fig. 3). The Sahel Acacia-wooded grassland and deciduous bushland forms the northern limit. *E. g. gambianus* is a woodland species that does not seem to avoid the forest edge (Bergmans, 1988). Specimens have been collected in the closed rainforest southwest of Kumasi (Ghana; Rosevear, 1965). There are three disjunctions in the range of *E. g. gambianus*: between 8°W in central Guinea to 12°W in southwestern Mali, between southwestern Chad and western Central African Republic, and between 23°E in the eastern Central African Republic and 32°E in southern Sudan (Bergmans, 1988; Fig. 3). Specimens of *E. g. pousarguesi* have only been collected in the Central African Republic (Andersen, 1912; Bergmans, 1978b, 1988). *E. g. crypturus* occurs from eastern Angola east to Kenya and southern Tanzania and south in parts of Namibia, Botswana, Malawi, Zimbabwe, Mozambique, and northeastern South Africa (Ansell, 1960a, 1978; Bergmans, 1988).

**ONTOGENY AND REPRODUCTION.** Adult females have two large pectoral mammae (Rosevear, 1965). Females collected in western Niger during the peak of the dry season (February through May) were either pregnant or lactating. Pregnant females were collected in February, March, and May, and embryos averaged 23 mm in length. Lactating females were taken in February. Weaning probably occurs when abundant food resources are available during the period of maximum vegetative growth in the summer (June through August) rainy season (Poché, 1975). In Upper Volta, pregnant females were captured in March (length of embryos, 23 to 39 mm), May (length of embryo, 49 mm), and September (Koopman et al., 1978). A lactating female with well-developed pectoral mammae was taken in January (Koopman et al., 1978). In Ghana, immature bats were reported in July, but detectably pregnant or



FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of mandible of male *Epomophorus gambianus*, National Museum of Natural History 377557, from Gambia. Greatest length of skull is 55.2 mm.

lactating females were absent. By the end of August the juveniles were approaching adult mass (Marshall and McWilliam, 1982).

*Epomophorus gambianus* may be classified as bimodally polyestrous with two parturition periods, followed by post-partum estrus, during the rainy season. Two birth and lactation periods occur annually and the timing of the breeding seasons may be determined by the need of food resources for the females for lactation rather than for the young after weaning. The first period of birth occurred in April, coinciding with the onset of the rainy season, and the second in October, the last rainy month. The first lactation period occurred during peak resources; the second followed 5 to 6 months later, due to the length of the gestation period, regardless of available resources. The gestation period is 5 to 6 months (Thomas and Marshall, 1984).

**ECOLOGY.** *Epomophorus gambianus* inhabits woodlands and savannas, and is common along forest edges and in the scrub of former forest belts (Happold and Happold, 1978; Kingdon, 1974; Rosevear, 1965). In southern Africa, the habitat of *E. g. crypturus* is the southern savanna woodland (Rautenbach, 1978).

It is likely that *E. gambianus* is an opportunistic forager on available fruit and nectar. In western Nigeria, *E. gambianus* was commonly observed when *Parkia* and mango trees (*Mangifera indica*) were flowering and when mangoes were fruiting, but less frequently at other times (Happold and Happold, 1978). Data from fecal samples showed that a greater number of food species were

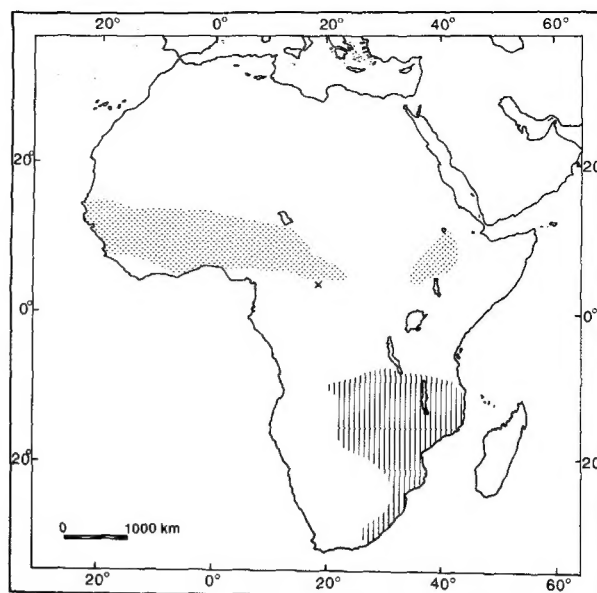


FIG. 3. Distribution of *Epomophorus gambianus* in Africa. Subspecies are *E. g. gambianus*, dotted area; *E. g. pousarguesi*, "X"; *E. g. crypturus*, vertical lines (modified from Bergmans, 1988).

utilized during the rainy season when resources were abundant than in the dry season. A total of eight species of fruit (species not given) was found in the feces of *E. gambianus* (Thomas and Marshall, 1984). The varied feeding habits of *E. gambianus* probably correlate with its occurrence in several vegetation zones (Rosevear, 1965). *E. gambianus* feeds on fruits of papaya (*Carica papaya*), mango (*Mangifera indica*), guava (*Psidium guajava*), cashew (*Anacardium occidentale*), and neem (*Azadirachta indica*). *E. gambianus* may be a dispersal agent for guava, cashew, and neem; *E. gambianus* has been observed leaving neem trees carrying the fruits. However, the relationship between *E. gambianus* and mango trees is a one-sided interaction; the bats were observed destroying as much as a third of the fruit while foraging, but did not seem to pollinate the flowers or disperse the fruit (Ayensu, 1974). *E. gambianus* has been observed foraging on *Adansonia digitata*, *Bombax* sp., *Ceiba pentandra*, *Diospyros senensis*, *Kigelia africana*, and *Terichilia emetica* (Poché, 1975; Rosevear, 1965; Thomas and Fenton, 1978). *E. gambianus* has been observed feeding on the nectar of *Parkia clappertoniana* (Baker and Harris, 1957; Harris and Baker, 1959). Bats collected while foraging on *P. clappertoniana* had pollen on the ventral and facial fur. Because bats only visited mature, intact inflorescences, pollen may be transferred between inflorescences. Although *E. gambianus* has been documented visiting *C. pentandra*, it may not be an important pollinator because peak foraging time for *E. gambianus* occurs before flowers of *C. pentandra* open (Baker and Harris, 1959). The divaricate scales on the hairs of nectar-feeding bats, including those of *E. gambianus*, may be adaptive for pollen collecting (Howell and Hodgkin, 1976). However, no significant correlation of hair structure and the eating habits of frugivorous and nectivorous bats when compared to insectivorous bats has been found (Thomas et al., 1984). There is no evidence that *E. gambianus* feeds on pollen or flower tissue. Nectar was found upon examination of stomach contents of *E. gambianus*, but pollen and anther tissue were not (Baker and Harris, 1957; Howell and Hodgkin, 1976).

*Epomophorus gambianus* roosts in a variety of trees, including *Khaya senegalensis*, *Kigelia africana*, *A. indica*, *Cola* sp., *Mangifera* sp., and *Ficus* sp. (Ayensu, 1974; Baker and Harris, 1957; Marshall and McWilliam, 1982; Poché, 1975; Rosevear, 1965; Thomas and Fenton, 1978). When roosting in a neem tree, the bats do not feed on the fruit of that particular tree (Ayensu, 1974). Records of the African Mammal Project in the National Museum of Natural History, Washington, D.C., indicate that *E. gambianus* was observed roosting with *Micropteropus pusillus* in a neem tree in Ghana. *E. g. crypturus* was observed roosting high in the tree canopy, 10 to 15 m above the ground (Thomas and Fenton, 1978). There are few records of predation on *E. gambianus*. Pied crows

(*Corvus albus*) have been observed to prey upon roosting bats during the day. However, *C. albus* may not be an efficient hunter of *E. gambianus* because predation was observed only when the crows were raising young (Smalley, 1984). A specimen in the British Museum is recorded as having been killed by a crow (Rosevear, 1965).

*Epomophorus gambianus* is known to be parasitized by *Hepatocystis epomophori* (Bray, 1984). *Listeria monocytogenes* was isolated from the feces of both *E. gambianus* and *Tadarida condylura*, which may be the first records of *L. monocytogenes* infecting bats (Höhne et al., 1975). Ectoparasitic insects have not been found on *E. gambianus* (Marshall and McWilliam, 1982; Pierce, 1984). Their absence may be due to the dispersed nature of the roosting colony, with individuals hanging at least 0.3 m apart (Marshall and McWilliam, 1982).

**BEHAVIOR.** *Epomophorus gambianus* roosts singly, in small groups of 12 to 20, and in large groups of >50 individuals (Happold, 1987; Marshall and McWilliam, 1982; Rosevear, 1965; Thomas and Fenton, 1978). They hang from small branches shaded by foliage (Happold, 1987). During observations made of roosting behavior of individuals in large roosts, males performed a piping call every 1 to 5 s, flapping their wings four times between calls while evaginating shoulder tufts. As other bats approached the call frequency doubled, and wing beats were amplified or the wings were held half-open and trembled (Marshall and McWilliam, 1982). The piping call also has been described as consisting of loud ringing honks every 2 to 3 s, accompanied by a flapping motion of the forearms. Individuals produced loud squawks and nasal honks when handled (Happold, 1987) and were vociferous when netted. During the day, *E. gambianus* roosts silently, occasionally grooming. Activity increases at dusk, with in-canopy flights and vocalizations, including the piping display and quarrelsome calls when territories are encroached (Ayensu, 1974; Marshall and McWilliam, 1982). Individual bats left the roost to forage between 1840 and 1900 h and returned from 0445 to 0515 h (Marshall and McWilliam, 1982). Flocks of roosting *E. gambianus* also have been observed to hover for 2 to 3 min, then leave en masse to forage (Ayensu, 1974).

*Epomophorus gambianus* generally feeds singly (Poché, 1975; Thomas and Fenton, 1978), but was observed feeding on *A. digitata* and *Butyrospermum paradoxum* in mixed-species flocks with *M. pusillus* and *Nanonycteris veldkampii*. In these observations, none of the bat flocks stayed more than 45 min; arrival and departure of the flocks were not synchronized. *E. gambianus* may not compete with *M. pusillus* and *N. veldkampii* due to timing of foraging as a result of commuting times from different roosts and to the other food resources available as a consequence of its larger size (Marshall and McWilliam, 1982). A female thought to be *E. gambianus* that exhibited communal behavior with *E. anurus* was collected in Ethiopia (Hill and Morris, 1971). *E. g. crypturus* was observed feeding with *Epomops dobsoni* and foraging on the same *Diospyros senensis* shrubs as *Rousettus aegyptiacus* (Ansell, 1960a; Thomas and Fenton, 1978). A gap in foraging time may serve as a basis for resource partitioning between *E. gambianus* and *R. aegyptiacus* (Thomas and Fenton, 1978).

Ayensu (1974) described the feeding behavior of *E. gambianus* on mango. As a bat approached a fruit, it reduced wing flapping and landed on the branch holding the fruit. It tore off the skin of the fruit and fed on the pulp until the flow of juices was reduced, at which time it moved to another fruit. *E. gambianus* lands, rather than hovers, to feed (Kingdon, 1974; Marshall and McWilliam, 1982). Feeding is silent, except for a few quarrelsome calls (Marshall and McWilliam, 1982).

When observed feeding on the nectar of *P. clappertoniana*, the bats had arrived at 1800 h, at the fading of daylight. Foraging was limited to the upper regions of the tree, where access to the inflorescences was the least obstructed. Grasping the inflorescence with its legs, an individual would push its snout into the nectar-holding depression and take nectar by lapping it with the tongue. Each visit to a flower lasted 15 to 45 s. Wings were used for balance, although the wings were sometimes wrapped partly around inflorescences. The visits of *E. gambianus* to the tree lasted about 20 min, until the arrival of *N. veldkampii*, which was observed to harass *E. gambianus*, causing it to fly away (Baker and Harris, 1957).

*Epomophorus gambianus* has been observed flying close enough to a river to wet the ventral fur, and it was suggested that the bat may later lick the wet fur to obtain water (Roussetot, 1950). This

possibility has been discounted due to insufficient evidence (Bergmans, 1978a).

**GENETICS.** *Epomophorus gambianus crypturus* has a diploid number of 35 chromosomes for males and 36 for females and a fundamental number of 68. Autosomes consist of six pairs of metacentrics, seven pairs of submetacentrics, and four pairs of subtelocentrics. A small, submetacentric chromosome is lacking in the male. It has an XX/XO sex chromosome system. Two other *Epomophorus* species (*E. wahlbergi* and *E. anurus*—now considered to be *E. labiatus*) have the same karyotype (Dulic and Mutere, 1973; Peterson and Nagorsen, 1975). The chromosome complement may be similar for all species of *Epomophorus*.

**REMARKS.** Ansell (1960a) described *E. g. parvus* as a subspecies of *E. gambianus*. *E. g. parvus* was differentiated from the nominate race by its smaller size; length of forearm (in mm) of males 82 to 85 for *E. g. parvus* and 87 to 98 for *E. g. gambianus*. Ansell (1960b) used the proportions of selected cranial measurements to differentiate *E. g. parvus* from *E. crypturus*. Ansell (1978) treated *E. g. parvus* as a separate subspecies, but expressed doubts regarding its status because of a lack of female specimens. He suggested that *E. gambianus* and *E. crypturus* may be conspecific, with *E. g. parvus* an intermediate subspecies, or that *E. g. parvus* may be a stage in a size cline. Honacki et al. (1982) and Meester et al. (1986) treated *parvus* as a subspecies of *E. crypturus*. Bergmans (1988) designated *crypturus* as a subspecies of *E. gambianus*, and synonymized *parvus* with *E. g. crypturus*. It is likely that a future systematic revision of *Epomophorus* will treat *crypturus* as a distinct species (C. Claessen, personal communication).

*Epomophorus reii* was described by Aellen (1950) based on the characters of palatal ridge structure and zygomatic width, *E. reii* having the fourth ridge closer to the third than the fifth and a zygomatic breadth that is greater than one-half of the total length of skull, whereas the fourth ridge of *E. gambianus* was midway between the third and fifth and the zygomatic breadth was less than one-half of the total length of skull (Aellen, 1950; Rosevear, 1965). Because the cranial measurements used by Aellen (1950) fall within the variation of *E. gambianus*, *E. reii* is now considered to be a variant of *E. gambianus* (Bergmans, 1988; Koopman, 1975). The fleshy palate of *E. reii* has not been preserved.

Hayman and Hill (1971) differentiated *E. gambianus* from *E. pousarguesi* by the position of the fourth palatal ridge, the ridge being closer to the third than the fifth in *E. pousarguesi*. Koopman (1975) considered *E. pousarguesi* to be a variant of *E. gambianus*. Bergmans (1978b), and later Koopman (1986), recognized *E. pousarguesi* as a subspecies of *E. gambianus*, suggesting that *E. pousarguesi* represents a marginal, perhaps isolated, population. This was supported by Bergmans (1988). However, examination of cranial and external body measurements shows that the few known specimens of *E. pousarguesi* fall near the upper limit of measurements of *E. g. gambianus*. This will negate the recognition of *E. pousarguesi* as a distinct subspecies of *E. gambianus* (C. Claessen, personal communication).

The generic placement of *grandis* had never been in doubt. It was treated as a part of *Micropteropus*. However, Bergmans (1988) proposed that it be recognized as a distinct species within *Epomophorus*. C. Claessen (personal communication) does not agree and in a soon-to-be published revision of *Epomophorus* will detail why *grandis* should remain in *Micropteropus*. *Epomophorus* is from the Greek words *epi* (upon), *omos* (shoulder), and *phoros* (bearing), referring to the conspicuous tufts of hair on the shoulders of males.

#### LITERATURE CITED

- AELLEN, V. 1950. Un megachiroptère nouveau, *Epomophorus reii* n. sp. *Revue Suisse Zool.*, 57:559–563.  
 ———. 1952. Contribution à l'étude des chiroptères du Cameroun. *Mem. Soc. Neuchateloise Sci. Nat.*, Neuchâtel, 8:1–121.  
 ANDERSEN, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. Second ed. Volume 1: Megachiroptera. Trustees British Mus. (Nat. Hist.), London, 854 pp.  
 ANSELL, W. F. H. 1960a. Some fruit bats from northern Rhodesia, with the description of a new race of *Epomophorus gambianus* Ogilby. *Rev. Zool. Bot. Africaines*, 61(1–2):160–166.  
 ———. 1960b. Mammals of Northern Rhodesia. Government Printer, Lusaka, Zambia, 155 pp.



- . 1978. The mammals of Zambia. National Parks Wildl. Serv., Chilanga, Zambia, 126 pp.
- AYENSU, E. S. 1974. Plant and bat interactions in West Africa. Ann. Missouri Bot. Garden, 61:702-727.
- BAKER, H. G., AND B. J. HARRIS. 1957. The pollination of *Parkia* by bats and its attendant evolutionary problems. Evolution, 11: 449-460.
- . 1959. Bat pollination of the silk cotton tree, *Ceiba pentandra* (L.) Gaertn. (sensu lato), in Ghana. J. West African Sci. Assoc., 5(1):1-9.
- BENNETT, E. T. 1836a. On a remarkable pteropine bat from the Gambia. Proc. Zool. Soc. London, 1835:149.
- . 1836b. On a remarkable species of pteropine bat. Trans. Zool. Soc. London, 2(1):31-38.
- BERGMANS, W. 1978a. Review of drinking behavior of African fruit bats (Mammalia: Megachiroptera). Bull. Carnegie Mus. Nat. Hist., 6:20-25.
- . 1978b. Rediscovery of *Epomophorus pousarguesi* Trouessart, 1904 in the Central African Empire (Mammalia, Megachiroptera). J. Nat. Hist., 12:681-687.
- . 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; material and methods; results: the genus *Epomophorus* Bennett, 1836. Beaufortia, 38:75-146.
- BOCAGE, J. V. B. 1899. Sur une nouvelle espèce de *Cynonycteris* d'Angola. J. Sci. Math., Physicas e Naturas, Lisboa, second ser., 5:133-140.
- BRAY, R. S. 1984. Some parasitic Protozoa from the Gambia. J. Protozool., 31:577-578.
- DEVREE, F. 1971. Note sur une collection de chiroptères Ouest Africains, principalement de la Côte d'Ivoire. Rev. Zool. Bot. Africaines, 83:31-49.
- DULIC, B., AND F. A. MUTERE. 1973. Les chromosomes de trois espèces des mégachiroptères (Mammalia, Chiroptera) d'Afrique orientale. Caryologia, 26:389-396.
- ERXLEBEN, I. C. P. 1777. Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium. Classis I. Mammalia. Weygandianis, Lipsiae, 636 pp.
- GEOFFROY SAINT-HILAIRE, I. 1828. Roussette. Pp. 695-708, in Dictionnaire classique d'histoire naturelle, 14:1-710.
- GRAY, J. E. 1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species. Mag. Zool. Bot., Edinburgh and Dublin, 2:483-505.
- HAPPOLD, D. C. D. 1987. The mammals of Nigeria. Clarendon Press, Oxford, 402 pp.
- HAPPOLD, D. C. D., AND M. HAPPOLD. 1978. The fruit bats of western Nigeria. Nigerian Field, 43:30-126.
- HARRIS, B. J., AND H. G. BAKER. 1959. Pollination of flowers by bats in Ghana. Nigerian Field, 24:151-159.
- HAYMAN, R. W., AND J. E. HILL. 1971. Order Chiroptera. Part 2. Pp. 1-73, in The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Inst. Press, Washington, D.C.
- HILL, J. E., AND P. MORRIS. 1971. Bats from Ethiopia collected by the Great Abba Expedition, 1968. Bull. British Mus. Nat. Hist. (Zool.), 21:25-49.
- HÖHNE, K., B. LOOSE, AND H. P. R. SEELIGER. 1975. Isolation of *Listeria monocytogenes* in slaughter animals and bats of Togo (West Africa). Ann. Microbiol. (Inst. Pasteur), 126A: 501-507.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Assoc. Syst. Coll., Lawrence, Kansas, 694 pp.
- HOWELL, D. J., AND N. HODGKIN. 1976. Feeding adaptations in the hairs and tongues of nectar-feeding bats. J. Morphol., 148: 329-336.
- KINGDON, J. 1974. East African mammals: an atlas of evolution in Africa. II(A): insectivores and bats. Academic Press, London, 446 pp.
- KOOPMAN, K. F. 1975. Bats of the Sudan. Bull. Amer. Mus. Nat. Hist., 154:353-444.
- . 1986. Sudan bats revisited: an update of "bats of the Sudan." Cimbebasia, 8A:9-13.
- KOOPMAN, K. F., R. E. MUMFORD, AND J. F. HEISTERBERG. 1978. Bat records from Upper Volta, West Africa. Amer. Mus. Novitates, 2643:1-6.
- MACLEAY, W. S. 1821. Horae entomologicae, or essays on the annulose animals, 1(1-2). Printed for S. Bagster, 1819-1821, London, 524 pp.
- MARSHALL, A. G., AND A. N. MCWILLIAM. 1982. Ecological observations on epomophorine fruit bats (Megachiroptera) in West African savanna woodland. J. Zool., London, 198:53-67.
- MATSCHIE, P. 1899. Die fledermäuse des Berliner Museums für Naturkunde. I. Megachiroptera. Georg Reimer, Berlin, 103 pp.
- MEESTER, J. A. J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Mus. Monogr., 5:1-359.
- Ogilby, W. 1835. Descriptions of Mammalia and birds from the Gambia. Proc. Zool. Soc. London, 3:97-107.
- PETERS, W. C. H. 1852. Naturwissenschaftliche reise nach Mozambique. Zoologie. I. Säugethiere, Berlin, 202 pp.
- PETERSON, R. L., AND D. W. NAGORSEN. 1975. Chromosomes of fifteen species of bats (Chiroptera) from Kenya and Rhodesia. Life Sci. Occas. Papers, Royal Ontario Mus., 27:1-14.
- PIERCE, M. A. 1984. Parasites of Chiroptera in Zambia. J. Wildl. Diseases, 20:153-154.
- POCHÉ, R. M. 1975. The bats of National Park W, Niger, Africa. Mammalia, 39:39-50.
- RAUTENBACH, I. L. 1978. A numerical reappraisal of the southern African biotic zones. Bull. Carnegie Mus. Nat. Hist., 6:175-187.
- RIDGWAY, R. 1912. Color standards and color nomenclature. Published by the author, 129 pp.
- ROSEVEAR, D. R. 1965. The bats of West Africa. Trustees of the British Mus. (Nat. Hist.), London, 418 pp.
- ROUSSELOT, R. 1950. Les roussettes du Soudan (animaux nuisibles). Comptes Rendus: Prem. Conf. Africanistes de l'Ouest, 1:233-238.
- SMALLEY, M. E. 1984. Predation by pied crows *Corvus albus* on Gambian epauletted fruit bats *Epomophorus gambianus*. Bull. British Ornithol. Club, 104:77-79.
- SWAINSON, W. 1835. On the natural history and classification of quadrupeds. Longman, Rees, Orme, Brown, Green, and Longmans, London, 397 pp.
- TEMMINCK, C. J. 1853. Esquisses zoologiques sur la Côte de Guinée, 1e partie, les mammifères. E. J. Brill, Leiden, 256 pp.
- THOMAS, D. W., AND M. B. FENTON. 1978. Notes on the dry season roosting and foraging behavior of *Epomophorus gambianus* and *Rousettus aegyptiacus* (Chiroptera: Pteropodidae). J. Zool., London, 186:403-406.
- THOMAS, D. W., AND A. G. MARSHALL. 1984. Reproduction and growth of three species of West African bats. J. Zool., London, 202:265-281.
- THOMAS, D. W., B. CRAWFORD, S. EASTMAN, R. GLAFSCHESKIE, AND M. HEIR. 1984. A reappraisal of the feeding adaptations in the hairs of nectar-feeding bats. J. Mamm., 65:481-484.
- TROUESSART, E. L. 1904. Catalogus mammalium tam viventium quam fossilium. Quinquennale Suppl., Parts 1 and 2, Berlin, Friedlander und Sohn, 546 pp.
- WAGNER, J. A. 1855. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber. Supplementband. L. D. Weigel, Leipzig, 5:810 pp.

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